

Dentition, diet and behaviour of six gobiid species (Gobiidae) in the Caribbean Sea

by

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ABSTRACT. - Using scanning electron microscopy (SEM) the upper and lower jaw and for the first time the pharyngeal jaw apparatus were described in *Coryphopterus dicrus* (Böhlke & Robins, 1960), *C. eidolon* (Böhlke & Robins, 1960), *C. thrix* (Böhlke & Robins, 1960), *C. tortugae* (Jordan, 1904), *C. venezuelae* (Cervigón, 1966) and *Gnatholepis thompsoni* (Jordan, 1904). The dentition of all *Coryphopterus* species was found to be quite similar in arrangement, number and shape. *Gnatholepis thompsoni* differs from the other species in the number of teeth and their arrangement as well as in its pharyngeal jaw apparatus where the bones are morphologically distinct in the lower jaw. The latter had been observed in other species of *Gnatholepis* and could therefore be a synapomorphy for the genus. Additionally, stomach contents analyses were performed to determine diet composition. All gobies feed primarily on benthic invertebrates and have a similar prey spectrum; species specific and individual differences were found for *Coryphopterus* species, whereas *Gnatholepis thompsoni* had an unspecialised diet. An overlap in diet and dentition as seen in *Coryphopterus* spp. suggests that they use distinct microhabitats and do not compete for food. Observations on their feeding behaviour indicate that differences exist between size and sex within species of *Coryphopterus* and external factors such as currents, wave action and suspended particles in the water column play a major role.

RÉSUMÉ. - Dents, régime alimentaire et comportement de cinq espèces de gobies (Gobiidae) des Caraïbes.

Les mâchoires supérieures et inférieures ainsi que les mâchoires pharyngiennes ont été observées au microscope électronique à balayage (SEM) et décrites pour la première fois pour *Coryphopterus dicrus* (Böhlke & Robins, 1960), *C. eidolon* (Böhlke & Robins, 1960), *C. thrix* (Böhlke & Robins, 1960), *C. tortugae* (Jordan, 1904), *C. venezuelae* (Cervigón, 1966) et *Gnatholepis thompsoni* (Jordan, 1904). L'arrangement, le nombre et la forme des dents sont très similaires chez toutes les espèces de *Coryphopterus*. En revanche, l'arrangement et le nombre des dents, ainsi que les mâchoires pharyngiennes, diffèrent chez *Gnatholepis thompsoni*. Ces différences ont été observées chez d'autres espèces de *Gnatholepis*, suggérant la présence d'une synapomorphie. Les contenus stomacaux ont également été analysés. Tous ces gobies se nourrissent principalement d'invertébrés benthiques et présentent un spectre de proies semblable. Il existe des différences non seulement entre les espèces mais aussi entre les individus ; c'est le cas pour les espèces de *Coryphopterus* qui, contrairement à *Gnatholepis thompsoni*, n'ont pas de régime alimentaire spécialisé. L'observation de leur comportement alimentaire montre des différences liées à la taille et au sexe des poissons ainsi qu'à des facteurs externes comme les courants, le mouvement de la mer et les particules en suspension dans la colonne d'eau.

Key words. - Gobiidae - *Coryphopterus* - *Gnatholepis* - ASW - Caribbean Sea - Dentition - Pharyngeal jaw apparatus - Scanning electron microscopy - Diet - Feeding behaviour.

The morphology of the skull and feeding apparatus, including the form and function of the teeth and the pharyngeal tooth plates play an important role in fish feeding behaviour, determine prey items and can be used as a base for phylogenetic comparisons (e.g., Galis and Drucker, 1996; Clifton and Motta, 1998; Parenti and Thomas, 1998; Larson, 2001; Westneat, 2006). The current study focuses on the oral jaws as well as the pharyngeal tooth plates of six Caribbean gobies living on sand. In fish the oral teeth are located on the dentaries in the lower jaw and on the premaxillary in the upper jaw. The pharyngeal tooth plates are situated in between the buccal cavity and the oesophagus, suspended from the neurocranium dorsally and bounded posteriorly and ventrally by the pectoral girdle (Wainwright, 2006).

Although the majority of studies have been on oral jaw apparatus, the pharyngeal tooth plates have an important role in processing foods and can even be considered to constrain the diet of certain groups of fish (Clifton and Motta, 1998). Scanning electron microscopy (SEM) was applied, which is a widely used technique for descriptive and comparative studies of teeth and feeding apparatus in gobies, blennies, cichlids and other fish species. Dentition can be linked to diet and gives an indication on how a fish feeds (e.g., Goldschmid *et al.*, 1980; Motta, 1985; Clifton and Motta, 1998; Parenti and Thomas, 1998; Pölzer and Patzner, 2000; Streelman *et al.*, 2003; Fishelson and Delarea, 2004; Greven *et al.*, 2005, 2006; Herler *et al.*, 2006; Ross *et al.*, 2006).

No information has been available on food resources of

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Coryphopterus dicrus, *C. thrix* and *C. venezuelae*, whereas *C. eidolon* is reported to feed primarily on benthic algae and other plants (Pattengill *et al.*, 1997). Analyses of the digestive tracts of *C. tortugae* – which, according to Baldwin *et al.* (2009), probably was *C. venezuelae* – found detritus, sand, filamentous algae, foraminifers, nematods and fish eggs (Garzón-Ferreira and Acero, 1990). An ecologically similar, congeneric species, *Coryphopterus cf. glaucofraenum* (see “Material and Methods” section for explanation), which is often found in the same type of habitats has been considered to be mainly herbivore and only to a lesser degree carnivore, showing bivalves, ostracods, ophiuroids and copepods among the prey items (Randall, 1967; Wayman, 1973). The same analysis for *Gnatholepis thompsoni* showed a similar result, with a large percentage of algae and detritus and a small proportion of copepods, amphipods, ostracods as well as unidentified crustaceans in the stomachs (Randall, 1967).

The goals of this study were to describe and compare dentition, prey items and feeding habits of six ecologically-related gobiids to find out if they rather share habitats and are specialised on different food or use the same food resources and occupy different microhabitats.

MATERIAL AND METHODS

The study site was a reef south of the Curacao Sea Aquarium, Curacao, Caribbean Sea (GPS coordinates + 12.08371 - 68.89645). Identifying *Coryphopterus* species had been problematic for certain species (Baldwin *et al.*, 2009); *C. tortugae* and *C. venezuelae* had been questioned as distinct species from *C. glaucofraenum* (e.g., Böhlke and Robins, 1960; Cervigón, 1966; Thacker and Cole, 2002), genetic analyses confirmed them to be clearly separated (Baldwin *et al.*, 2009). Former studies which have presented results on *C. glaucofraenum* are therefore referred to *C. cf. glaucofraenum* in this paper because it is uncertain if the species was *C. glaucofraenum*, *C. tortugae* or *C. venezuelae*; according to the common keys, they had not been regarded as different species (Böhlke and Robins, 1960; Böhlke and Robins, 1962; Böhlke and Chaplin, 1968; Murdy, 2002).

For identification of fish species DNA barcodes (650 bp of the mitochondrial gene cytochrome c oxidase I) were obtained and compared with the database of *Coryphopterus* COI sequences compiled at the Smithsonian Institution in Washington, D.C. for the revisionary work on western Atlantic *Coryphopterus* by Baldwin *et al.* (2009). Extracting and sequencing of DNA was performed according to Baldwin *et al.* (2008).

For the study of their dentition, the following fish were used [Standard Length = SL]:

1) Eight individuals of *Coryphopterus dicrus*, which genetically separated into two clades: *C. dicrus*_1: four

females [SL = 2.2 cm; 2.3 cm; 2.3 cm; 2.4 cm] and one male [SL = 1.8 cm] and *C. dicrus*_2: two females and one male [SL = 2.4 cm; 2.4 cm; 2.4].

2) Eleven individuals of *C. eidolon*: five females [SL = 2.6 cm; 2.8 cm; 2.9 cm; 3.2 cm; 3.5 cm], two males [SL = 3.6 cm; 3.7 cm] and three individuals which had not been sexed [SL = 3.8 cm, 4.1 cm, 4.4 cm].

3) Seven individuals of *C. thrix*: five females [SL = 2.1 cm; 2.4 cm; 2.4 cm; 2.6 cm; 2.6 cm] and two males [SL = 2.4 cm; 2.7 cm].

4) Seven individuals of *C. tortugae*: five males [SL = 4.3 cm, 4.6 cm, 4.8 cm, 4.8 cm, 5.0 cm] and two females [SL = 2.5 cm; 3.5 cm].

5) Seven individuals of *C. venezuelae*: five females [LS = 2.8 cm, 2.9 cm, 3.0 cm, 3.3 cm, 3.6 cm], one juvenile [LS = 2.4 cm] and one male [LS = 5.0 cm].

6) Seven individuals of *Gnatholepis thompsoni*: five females [LS = 1.9 cm; 2.3 cm; 2.4 cm; 2.9 cm; 3.7 cm] and two males [LS = 1.9 cm; 2.0 cm].

The fish were anaesthetized with Quinaldine and caught with hand nets. They were put on ice, measured, weighed and sexed. Their heads were preserved in 5% formaldehyde for approximately two weeks and then transferred to alcohol (70%). Then they were put into a solution of approximately 1:5 of cleaning detergent (Ecover©) in water and kept at a temperature of 37°C until the tissue could be removed from the bones. The skulls were cleaned with alcohol and dried at 37°C for two weeks. For SEM investigation, the skulls and jaws were mounted with liquid silver (Emeton©) on aluminium specimen stubs, sputtered with gold and investigated with a Philips XL 30 ESEM scanning electron microscope.

For studies and drawings of pharyngeal tooth plates five stained and cleared fish from the collection of the American Museum of Natural History (AMNH) in New York, USA were used: *C. dicrus* (AMNH 33593), *C. eidolon* (AMNH 34942), *C. thrix* (AMNH 33597), *C. tortugae* (AMNH 243327) and *C. venezuelae* (AMNH 243327). Their pharyngeal tooth plates were studied under a binocular microscope.

The following specimens were analysed for stomach contents: 39 individuals of *C. venezuelae* (SL = 2.4-5.1 cm), 18 individuals of *C. thrix* (SL = 2.3-3.5 cm), 7 individuals of *C. tortugae* (SL = 3.2-6.2 cm), *C. dicrus* divided into two genetically different clades: 20 individuals of *C. dicrus*_1 (SL = 2.0-3.8 cm), 6 individuals of *C. dicrus*_2 (SL = 2.5-3.5 cm), 36 individuals of *C. eidolon* (SL = 1.5-5.3 cm) and 21 individuals of *G. thompsoni* (SL = 1.3-5.4 cm). Bodies were preserved in 10% formaldehyde and stored in 70% ethanol.

Their digestive tract was opened and its contents placed in a Petri dish and identified under a stereoscope and/or compound microscope. Prey items were counted and the frequency of occurrence (% F-Value) as well as the percentage composition by number calculated (Hynes, 1950; Windell

and Bowen, 1978; Berg, 1979). Prey importance, feeding strategy and components of niche width were analysed graphically with the modified Costello (1990) method by Amundsen *et al.* (1996).

For behavioural studies ten individuals of different sizes, 2 or 3 of each species (*C. dicrus*, *C. eidolon*, *C. cf. glaucofraenum*, *C. thrix* and *G. thompsoni*) were observed underwater. Individual fish were chosen for observation based on having distinct attributes (i.e. size, species) and occurring at an easily recognizable location. This allowed us to be relatively certain we were observing the same fish each time without its being tagged. This technique did not work for *G. thompsoni*, which moves over large distances and occupies numerous shelters. Hence data for that species was collected by observing individuals of similar size. The total length (TL) of each fish was estimated visually. Two individuals of *C. dicrus* (TL = 2.5 cm; 5 cm), two individuals of *C. thrix* (TL = 5 cm), three individuals of *C. eidolon* (TL = 2 cm; 4 cm; 5 cm) and various individuals of *G. thompsoni*, all of the same size range (TL = 3 to 4.5 cm) were chosen for observation.

Coryphopterus species are protogynous hermaphrodites; the smaller individuals chosen for the observations were generally females and the larger individuals males, this was confirmed by observing typical behaviour of males/females e.g. courtship behaviour or fanning eggs, or a swollen abdomen in females exhibited before laying eggs, *G. thompsoni* is not protogynous (Cole, 1988, 1989; Cole and Shapiro, 1990) and therefore its sex could not be determined by size, nor does it show typical male/female behaviour.

All observations lasted for 20 minutes. A diver positioned a distance of 1-2 m away from the fish taking notes on the behaviour; recording if the fish was feeding from the substrate or the water column (Behrents Hartney, 1989). Each fish was observed eighteen times in total, six at each of three specific times during the day (07:00-08:30, 12:00-13:30, 16:30-18:00), to observe if behaviour varied with the time of day. Conditions (waves, currents, visibility) were recorded. The number of movements (from one position into the next one) and the number of interactions with conspecifics were

counted and the total distance covered during the observation was estimated. To calculate the approximate area that a fish used during an observation, the observer measured a radius for an approximated circular area in which the fish had been moving and the surface of that area was calculated ($A = r^2\pi$). At the end of each observational cycle, after 18 observations, the home range for each fish was estimated by the observers. A chi-square test (phi, Cramer's V) was performed with SPSS 12.0.0 to test for a possible correlation between feeding activity and time of the day.

RESULTS

Genetic analysis

The genetic study confirmed that *C. tortugae* occurs in Curacao; it had not been reported from there before. *C. dicrus* separated into two different clades, which will require further studies to determine in how far these differ; in the present study no differences in dentition or stomach contents were found.

Dentition

No difference was detected between the genetically different *C. dicrus*_1 and *C. dicrus*_2, so the following description and photographs are valid for both and referred to as *C. dicrus*. Upper jaw (Fig. 1A, 1B): the premaxillae carry four to five rows of teeth. The most anterior row is enlarged and an edentulous gap is visible in the centre. All teeth are bent towards the buccal cavity and decrease in height from anterior to posterior. The outer row protrudes slightly over the inner rows. Towards the posterior end of the premaxillae, teeth become smaller, thinner and the number of rows decreases; at the caudal end of the premaxillae there is only one row of teeth left. Results of teeth counts are listed in Tab. I. Lower jaw (Fig. 1C, 1D): the dentaries consist of 12 to 13 enlarged frontal canines, which protrude about two to three times in its length over a band of four to five rows of smaller caniniform teeth which lie posteriorly. The innermost row of those teeth is more elongated than the anterior

Table I. - Number of teeth counted in *Coryphopterus* and *Gnatholepis* species. n: Number of individuals sampled. LS: Standard length.

Species	n	LS [cm]	Number of teeth upper jaw		Number of teeth lower jaw		Number of enlarged front teeth lower jaw		Number of teeth PJA-upper jaw		Number of teeth PJA-lower jaw	
			range	mean	range	mean	range	mean	range	mean	range	mean
<i>C. dicrus</i> _1	5	1.8-2.4	180-220	200 ± 16	132-182	156 ± 23	9-14	12 ± 2	64-70	71 ± 6	56-64	59 ± 3
<i>C. dicrus</i> _2	3	2.4	188	188	133-198	158 ± 35	13-16	17 ± 2	-	-	-	-
<i>C. eidolon</i>	11	2.6-4.4	200-290	246 ± 29	140-192	169 ± 16	9-14	11 ± 2	76-100	89 ± 9	70-88	79 ± 8
<i>C. thrix</i>	7	2.1-2.7	136-246	168 ± 47	122-214	149 ± 32	9-13	11 ± 1	48-124	77 ± 33	47-56	53 ± 4
<i>C. tortugae</i>	7	2.4-4.2	252-290	278 ± 13	128-246	210 ± 42	14-19	15 ± 2	72-102	87 ± 21	116	116
<i>C. venezuelae</i>	7	2.5-5.0	240-274	253 ± 31	154-190	171 ± 17	13-19	15 ± 2	84	84	86-88	87 ± 1
<i>G. thompsoni</i>	6	1.9-3.7	64-82	74 ± 7	42-52	48 ± 4	(6-9)+2	7 ± 1	150	150	140	140

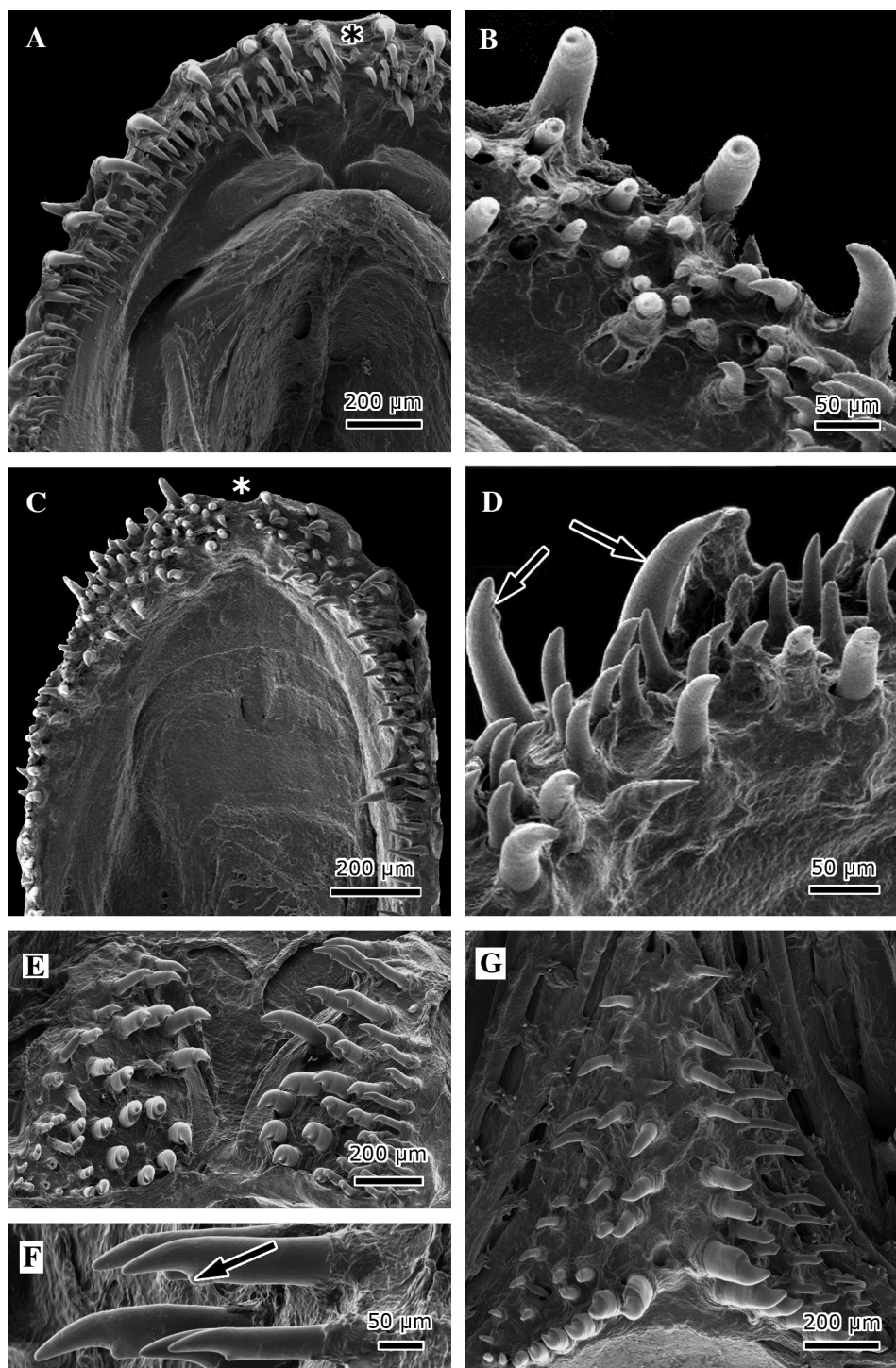


Figure 1. - Dentition in oral and pharyngeal jaws in *Coryphopterus dicrus*. **A**: Upper oral jaw; the asterisk shows an edentulous gap. **B**: Detail of upper oral jaw. **C**: Lower oral jaw; the asterisk shows an edentulous gap. **D**: Detail of lower oral jaw; arrows indicate two caniniform teeth. **E**: Teeth of upper pharyngeal jaw. **F**: Detail of teeth on upper pharyngeal jaw, the arrow indicates a ridge with bulge at caudal side of tooth. **G**: Teeth of lower pharyngeal jaw.

rows. A small edentulous gap can be seen in the centre region (Fig. 1C). All teeth have a pointed apex which is bent towards the buccal cavity. The number of rows decreases

towards the posterior side of the dental components until only one row of thin, enlarged teeth is left. Approximately, it can be divided into five to six rows of teeth in the anterior

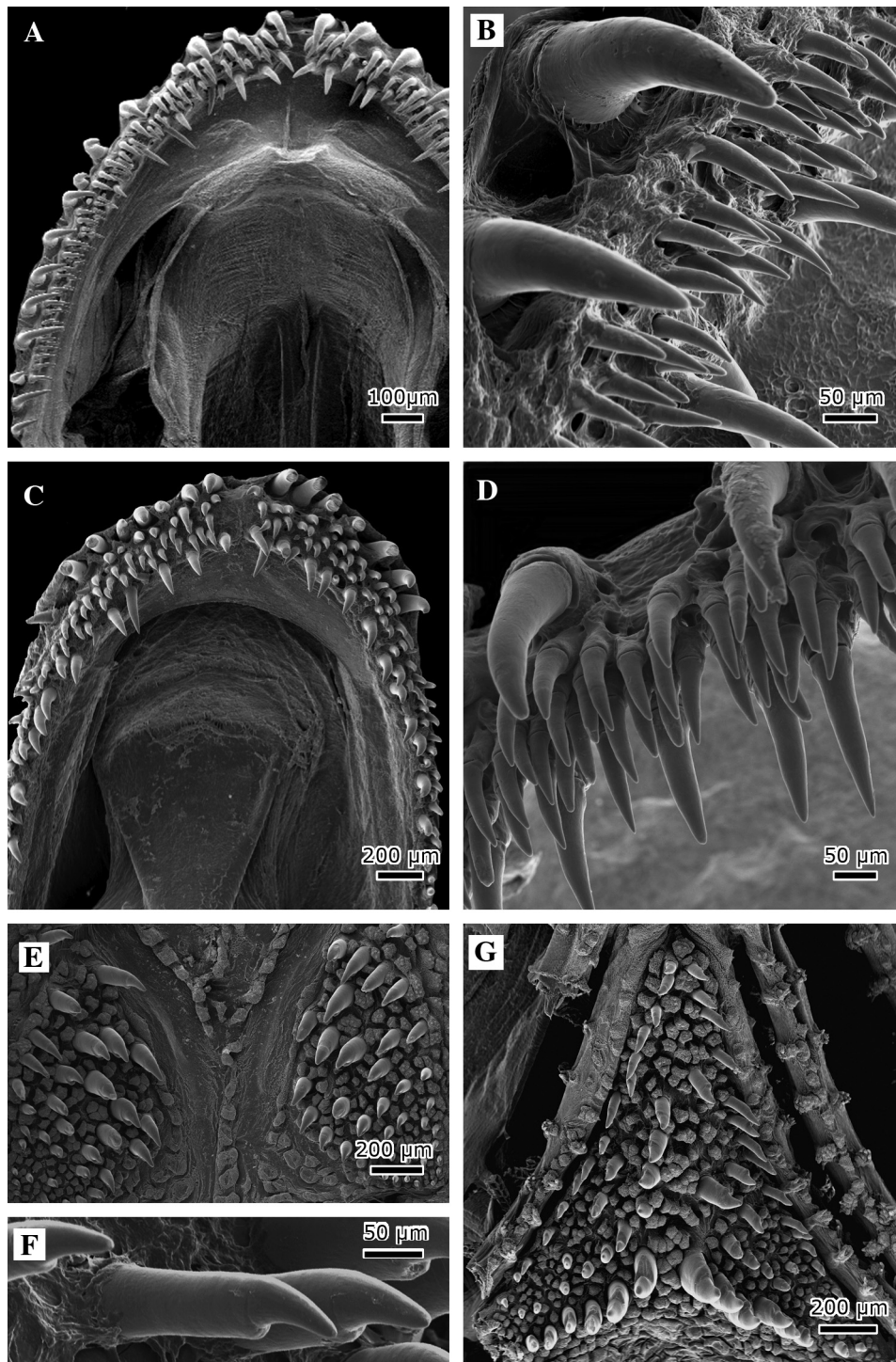


Figure 2. - Dentition in oral and pharyngeal jaws in *Coryphopterus eidolon*. A: Upper oral jaw. B: Detail of teeth on the upper oral jaw. C: Lower oral jaw. D: Detail of teeth on the lower oral jaw. E: Teeth of upper pharyngeal jaw. F: Detail of teeth on upper pharyngeal jaw. G: Teeth of lower pharyngeal jaw.

third of the mouth, two rows on the sides, which would be the medium region: in the posterior third of the mouth only one row of teeth exists.

A difference could be found among two females and one

male fish with the same size (all three fish were *C. dicrus_2*). Both females had five rows of teeth in the front part of their lower jaw, whereas the male had 6 rows. The number of rows in the upper jaw was identical. In the second examined male

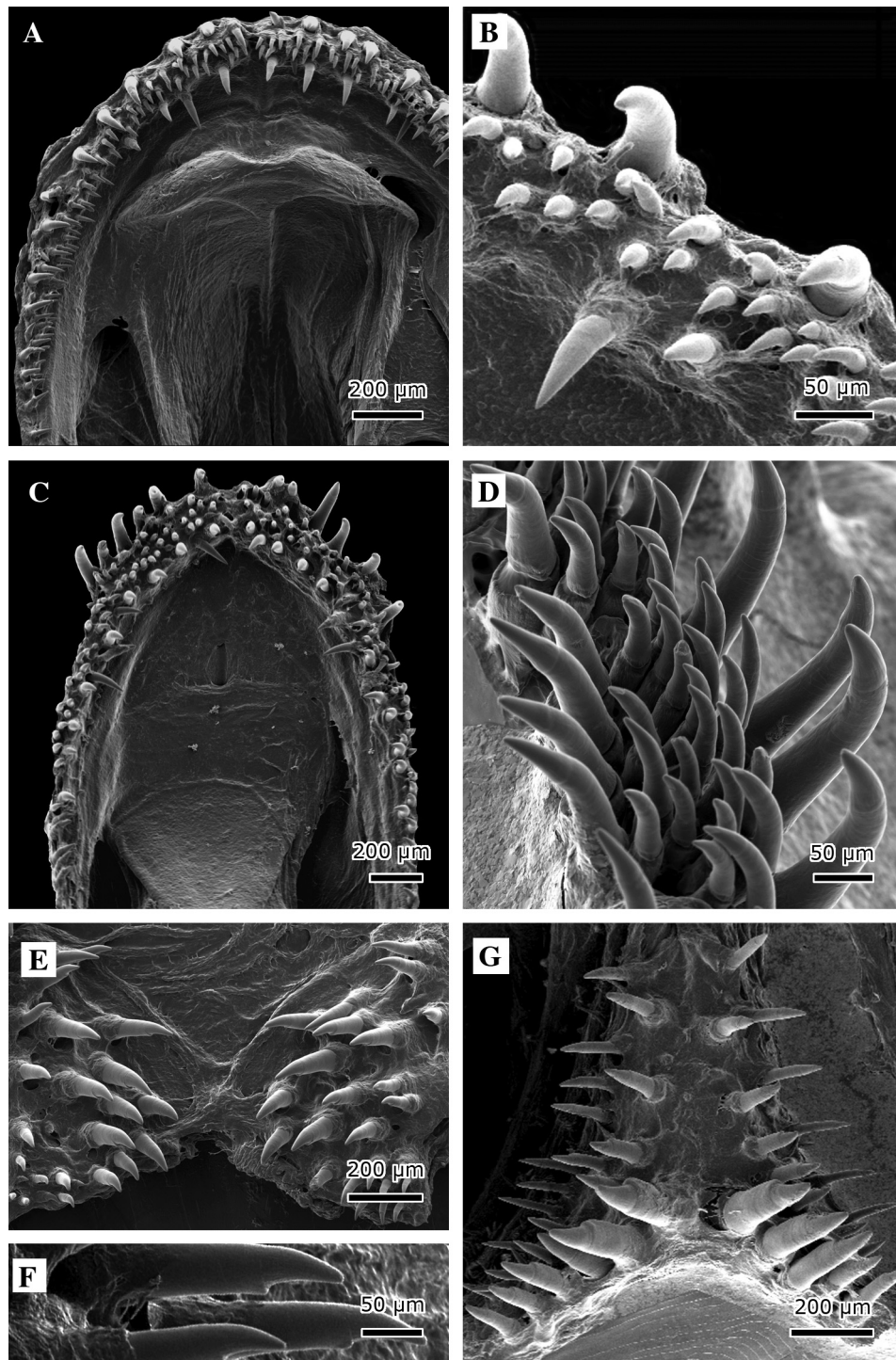


Figure 3. - Dentition in oral and pharyngeal jaws in *Coryphopterus thrix*. **A:** Upper oral jaw. **B:** Detail of teeth on the upper oral jaw. **C:** Lower oral jaw. **D:** Detail of teeth on the lower oral jaw. **E:** Teeth of upper pharyngeal jaw. **F:** Detail of teeth on upper pharyngeal jaw. **G:** Teeth of lower pharyngeal jaw.

(*C. dicrus_1*), which was smaller, the same number of teeth rows as in the females was observed.

Pharyngeal tooth plates (Fig. 1E-1G): in the upper jaw, two dentigerous elements can be found (Fig. 1E). Each of

them consists of three elements which are joined by connective tissue. The largest teeth are at the front which is the anterior rim of the tooth plates and their size decreases towards the outer caudal end of the plate. The smallest teeth in that

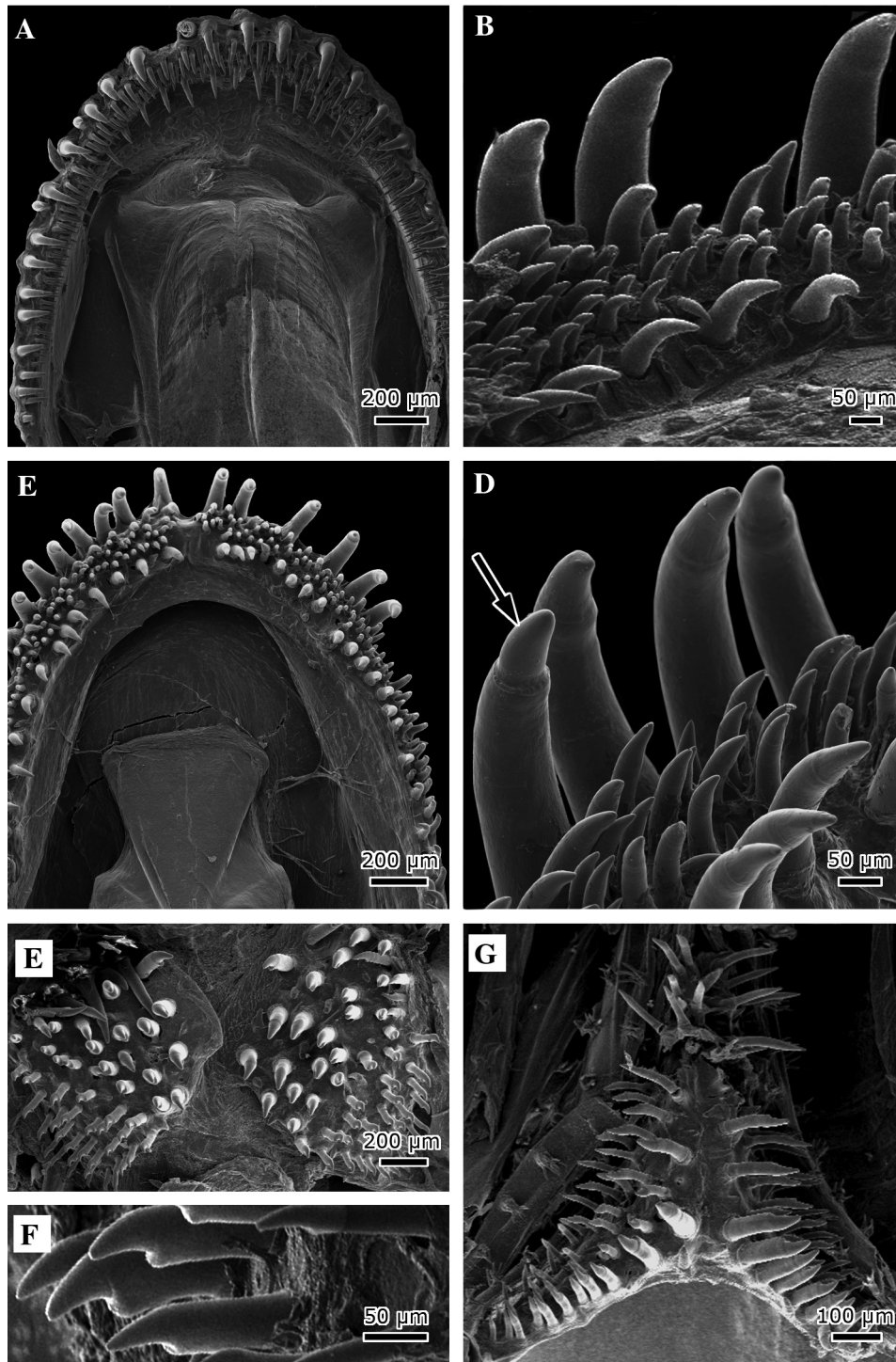


Figure 4. - Dentition in oral and pharyngeal jaws in *Coryphopterus tortugae*. **A:** Upper oral jaw. **B:** Detail of upper oral jaw. **C:** Lower oral jaw. **D:** Detail of teeth on lower oral jaw; the arrow indicates a conical cusp. **E:** Teeth of pharyngeal upper jaw. **F:** Detail of teeth on pharyngeal upper jaw. **G:** Teeth on pharyngeal lower jaw.

region are 25 to 33% the height of the largest teeth at the anterior, cranial end of the tooth plates. Teeth are bent buccally, laterally compressed and show a concavity towards the posterior side of the tooth, thus resembling hooks (Fig. 1F).

In the lower jaw, the two separated pharyngeal tooth plates are located on the fifth ceratobranchial bones and together form a triangular, dentigerous element, pointing to the opening of the mouth (Fig. 7). Towards the posterior end and the

centre of dentigerous element, teeth increase in diameter and change their shape. The outer rows of teeth are slimmer and less structured, whereas the posterior rows of teeth are laterally compressed and have edges below their bent cusps. In the larger teeth there is a small ridge with a visible bulge at their caudal side pointing in the same direction as the tooth cusp. The anterior rows of teeth show a very pointed apex, whereas the thicker, posterior teeth have cusps with a wider base and are less pointed. All apices are bent towards the buccal cavity. The largest teeth (in both, length and diameter) can be seen in the center of the posterior rim of the pharyngeal tooth plate. Their size decreases notably towards the edges of the tooth plates (Fig. 1G).

For *C. eidolon*, the arrangement and sizes of teeth are more or less similar as in *C. dicrus*. The upper jaw has five rows of teeth, in which the first and the fifth row are protruding over the three rows in between (Fig. 2A, 2B, Tab. I). The lower jaw bears four rows in the small-sized individuals and five rows in the ten large-sized individuals (Fig. 2C, 2D). The number of teeth does not relate to sex or size of the fish. The dentigerous elements, on which the pharyngeal tooth plates are located and their arrangement in the upper and in the lower jaw are the same as observed in *C. dicrus* (Fig. 2E-2G).

In both the lower and the upper jaws of *C. thrix* has five rows of canine teeth. Arrangement and shape of the teeth are similar to the previously mentioned species and declining in number towards the caudal end (Fig. 3A-3D). Results of teeth counts are listed in table I. Teeth in the pharyngeal tooth plates do not show any significant difference to *C. dicrus* or *C. eidolon* (Fig. 3E-3G), no differences between male and female fishes were found. Arrangement, shape and number of teeth for *C. tortugae* are similar as in *C. dicrus*, *C. eidolon* and *C. thrix* with five to eight rows in both the upper and lower jaws (Fig. 4A-4D). Results of teeth counts are listed in table I. The two females, which were smaller in size, had a clearly lower number of teeth in the lower jaw. In the large individuals, the canine teeth show a division into base and conical cusp (Fig. 4D). Regarding the pharyngeal teeth, the lower pharyngeal tooth plate shows no differences to the other *Coryphopterus* species (Fig. 4E-4G). For *C. venezuelae*, arrangement, shape and number of teeth were similar to previous species with four to five rows in both the upper and lower jaws (Fig. 5A-5D). No differences between males and females were found.

In the upper jaw of *Gnatholepis thompsoni*, 1 or 2 rows of small teeth are bordered by one row of large teeth. The frontal (most anterior) teeth are the longest and most bent, results of teeth counts are listed in table I. Those frontal teeth are about one third longer than the other teeth in the outermost row and about four times the length of teeth in the inner rows (Fig. 6A, 6B). The dentaries of the lower jaw (Fig. 6C, 6D) carry only one row of small teeth; on its outside there

are between seven and eleven large, widely spaced canini-form teeth. The most posterior of those enlarged teeth, on either side, is clearly longer and bent more caudally, resembling a fang. These two teeth have about 4 times the length of the small teeth; the other teeth of the outer row have about three to four times the length of the small teeth. No difference in dentition between males and females could be found.

Pharyngeal tooth plates (Fig. 6E-6G): in the lower jaw, teeth are located on a triangular dentigerous element with its "peak" orientated towards the mouth opening. The tooth plates are situated together closely and interdigitated on the ventral side. The teeth are strongest in the centre of the caudal-most part. The cusps are more rounded than pointed, showing a somewhat hooked shape, with a thick and laterally flattened apex.

The upper pharyngeal tooth plates are placed on two dentigerous elements. Their arrangement is similar to the pharyngeal teeth of *Coryphopterus* spp. with the longest and thinnest teeth in the anterior part. These teeth are small toward the outer and posterior rims and thick toward the central posterior end of the plates. The apices of all teeth are bent towards the pharynx in a hook like manner. A slight bifurcation can be noted especially in the slimmer teeth of the anterior part of the tooth plates. In the posterior teeth, the teeth seem flattened and the bifurcation has been cut in an angle of approximately 45° (Fig. 6F). Results of teeth counts are listed in table I.

Diet analysis

The dominant food type was copepods, which were present in most of the species and in the largest quantities, relative to other prey types. The diet mainly consisted of benthic associated invertebrates (Copepoda, Amphipoda, Tanaidae, UnID Malacostraca, Isopoda, Ostracoda, UnID Crustacea, Polychaeta, Nematoda, Bivalvia, Gastropoda) (Tab. II, Fig. 8). *G. thompsoni*'s most numerous preys, after copepods, were nematodes and ostracods, which were rarely present in *Coryphopterus* species. Graphical analysis (Fig. 9) of feeding data (except for *C. dicrus_2* where not enough data were available) indicate that the species are generalized feeders having a broad niche width (prey points located around the lower left of the diagram), with all populations of fish specialised towards copepods, especially *C. dicrus_1*, *C. tortugae* and *G. thompsoni* (prey points in the upper right half) and one individual of *Coryphopterus thrix* specialised on unidentified Malacostraca (prey point at the upper left). The diagram of *G. thompsoni* differs from *Coryphopterus* spp. by prey points being very close or on the x-axis, showing very low specific abundance of prey items, and towards the right of the diagram, representing prey eaten occasionally by most individuals. The latter indicates a higher within phenotype component; meaning that many individuals use

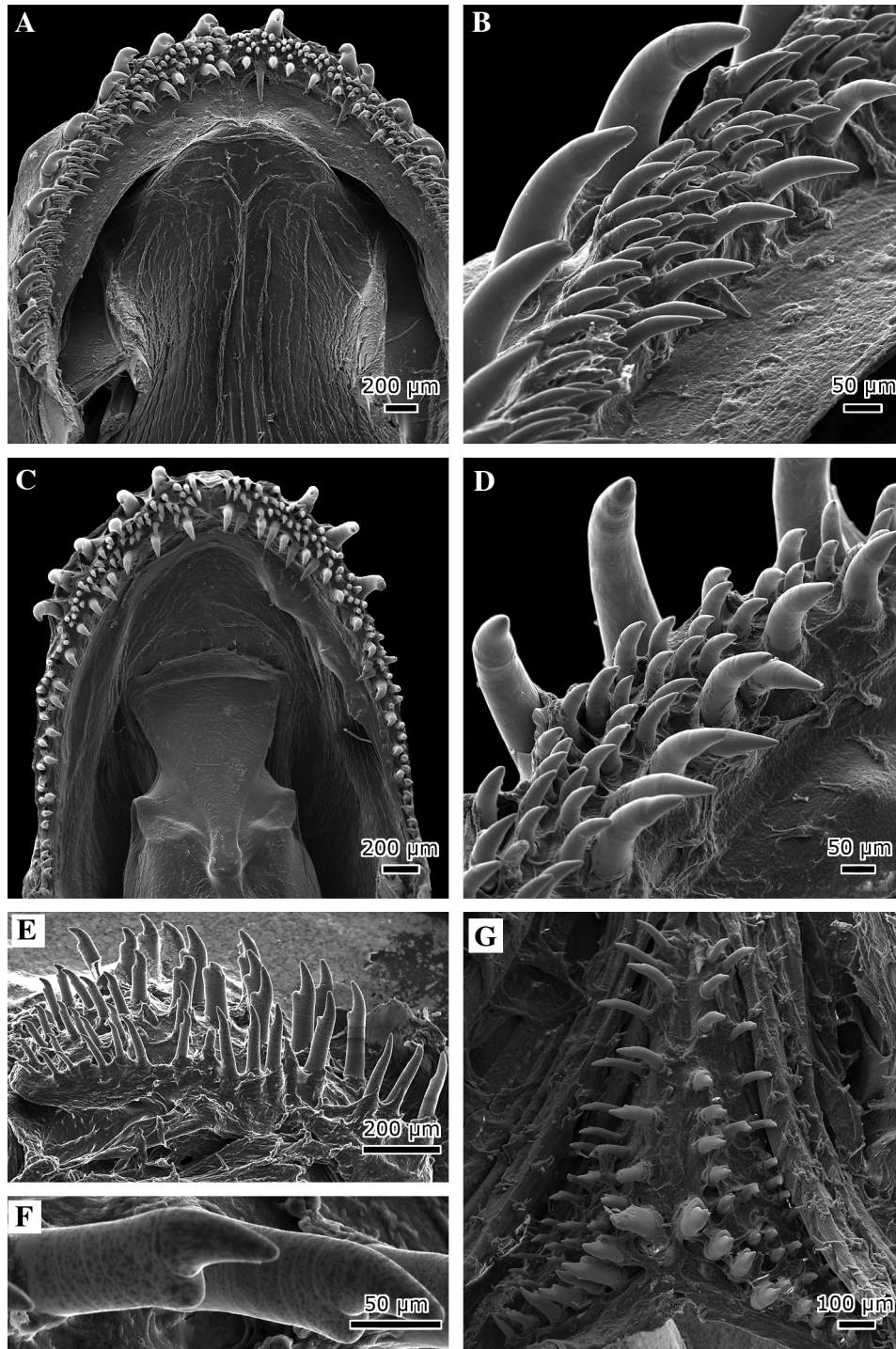


Figure 5. - Dentition in oral and pharyngeal jaws in *Coryphopterus venezuelae*; **A**: Upper oral jaw. **B**: Detail of upper oral jaw. **C**: Lower oral jaw. **D**: Detail of lower oral jaw. **E**: Teeth of upper pharyngeal jaw. **F**: Detail of teeth on pharyngeal upper jaw. **G**: Teeth of pharyngeal lower jaw.

various resources simultaneously; whereas in *Coryphopterus*, especially *C. thrix*, the between phenotype component is high, indicating that individuals are specializing in different food types. *G. thompsoni*'s prey point on the x-axis at the far

right represents unidentified material, present in 95% of the stomachs and indicating that detritus might be a significant food source.

Analysing the frequency of occurrence (% F), the follow-

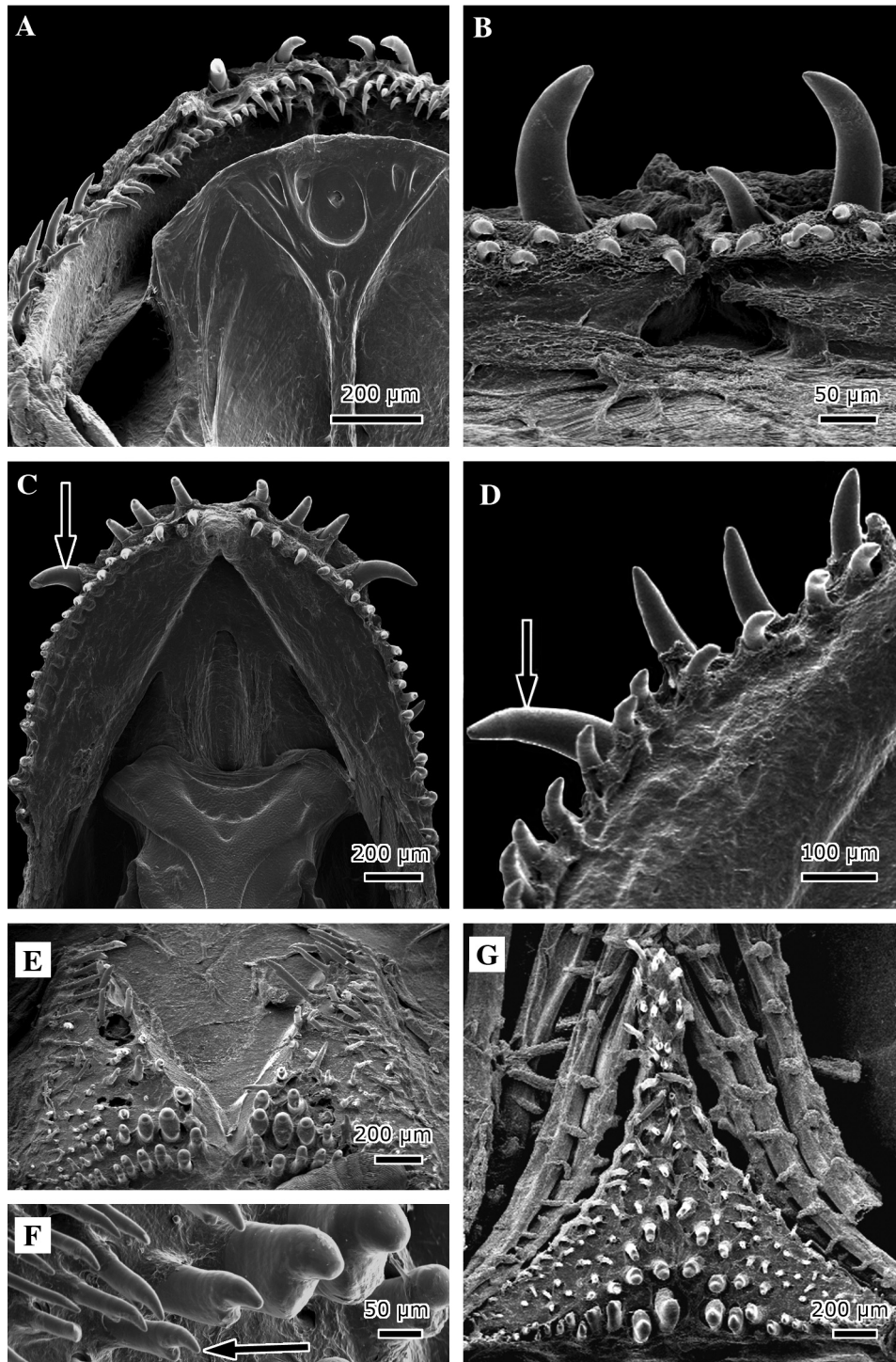


Figure 6. - Dentition in oral and pharyngeal jaws in *Gnatholepis thompsoni*. **A:** Upper oral jaw. **B:** Detail of upper oral jaw. **C:** Lower oral jaw; the arrow indicates a “fang-like” tooth. **D:** Detail of lower oral jaw; the arrow indicates a “fang-like” tooth. **E:** Teeth of pharyngeal upper jaw. **F:** Detail of teeth on pharyngeal upper jaw; the arrow indicates a bifurcation. **G:** Teeth of pharyngeal lower jaw.

ing conclusions can be drawn: (i) an important prey item for *C. eidolon* are Myscidiacea (44% F) which were also found in smaller quantities in *C. thrix* and *C. dicrus* 1 (15% F and 10% F), (ii) only *C. venezuelae* diet consisted of parts of fish

(5% F), (iii) the genetically distinct types of *C. dicrus* do not show differences in their ingested food, but a larger samples size is required to confirm this, (iv) *C. thrix* did not ingest sand along with its prey unlike all other species; large quan-

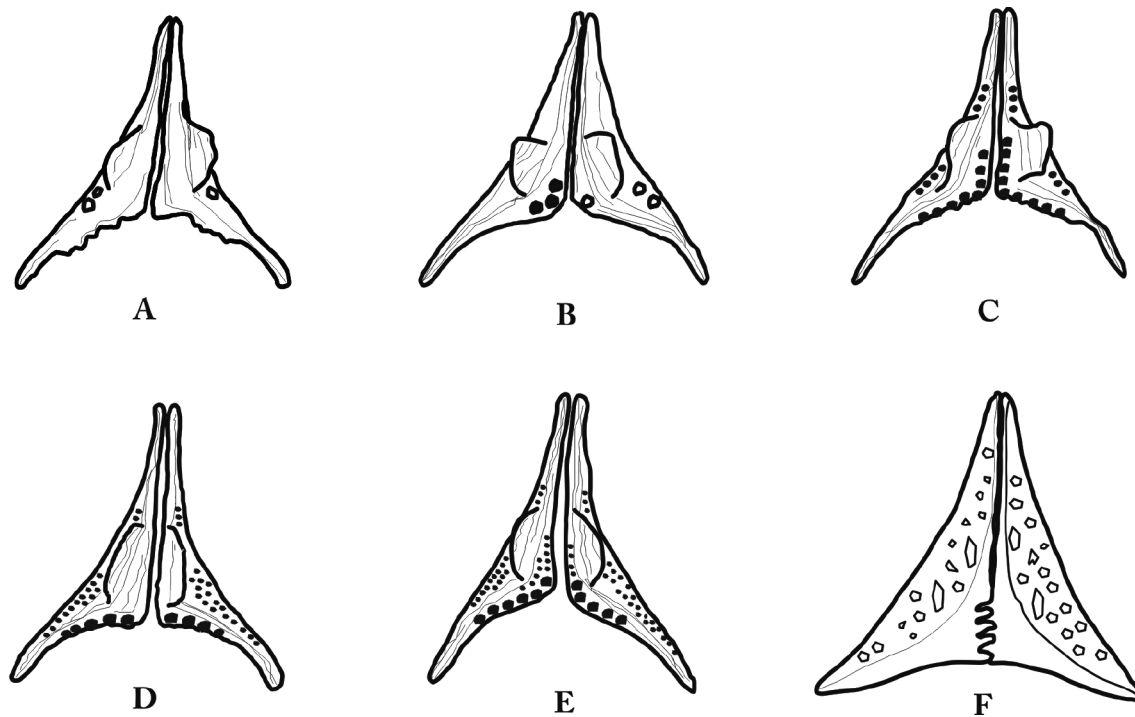


Figure 7. - Dorsal view of the lower pharyngeal jaw apparatus. A: *Coryphopterus dicrus*. B: *C. eidolon*. C: *C. thrix*. D: *C. tortugae*. E: *C. venezuelae*. F: *Gnatholepis thompsoni*. Tooth plates in *Coryphopterus* spp. are clearly separated, while in *Gnatholepis thompsoni* they are interdigitated and perforated.

Table II. - Frequency of occurrence (%) and percentage of stomachs which contained a specific food item for *Coryphopterus dicrus_1*, *C. dicrus_2*, *C. eidolon*, *C. thrix*, *C. tortugae*, *C. venezuelae* and *Gnatholepis thompsoni*. Algae and sand are not considered as food items, as they were ingested accidentally.

	<i>C. dicrus_1</i>	<i>C. dicrus_2</i>	<i>C. eidolon</i>	<i>C. thrix</i>	<i>C. tortugae</i>	<i>C. venezuelae</i>	<i>G. thompsoni</i>
n	20	4	27	13	7	38	21
Copepoda	65	100	52	46	86	50	81
Amphipoda	20	0	19	8	43	5	38
Tanaidae	15	50	19	15	29	21	0
Myscidaea	10	0	44	15	0	0	0
Isopoda	20	0	4	0	14	8	5
Ostracoda	0	0	7	0	0	3	24
UnID Malacostraca	32	0	7	8	0	18	0
UnID Crustacea	10	0	52	46	57	32	33
Polychaeta	0	0	22	0	0	5	0
Nematoda	0	0	7	0	14	5	71
Bivalvia	0	0	0	0	0	3	0
Gastropoda	0	0	4	0	0	0	0
UnID inverts	0	0	4	0	29	3	5
Teleostei	0	0	0	0	0	5	0
Algae	30	25	11	8	43	5	19
Sand	20	25	4	0	14	29	24
UnID material	50	25	52	38	43	37	95

ties of sand being found in the intestines of *C. dicrus* and *C. venezuelae*, and (v) despite high % F in some species, fil-

amentous algae were found in all species in very small quantities and are considered to be co-ingested with prey.

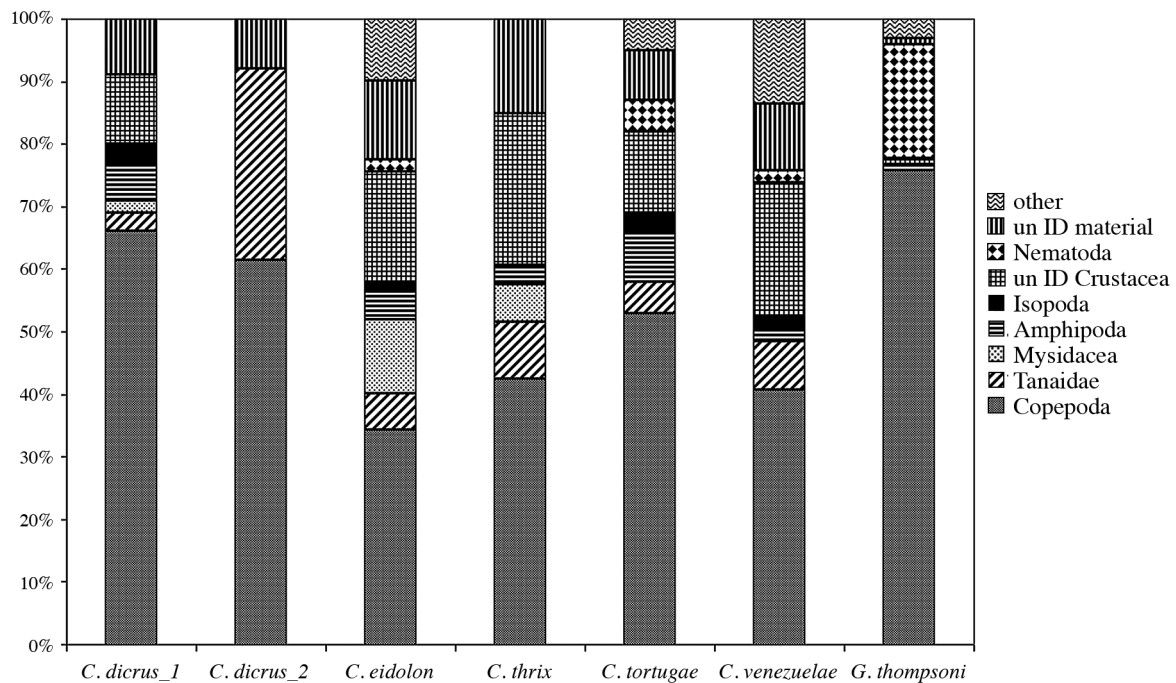


Figure 8. - Percentage composition of diet by numbers for *Coryphopterus dicrus_1*, *C. dicrus_2*, *C. eidolon*, *C. thrix*, *C. tortugae*, *C. venezuelae* and *Gnatholepis thompsoni*. Values for algae and sand were not taken into account as they are considered to be ingested accidentally.

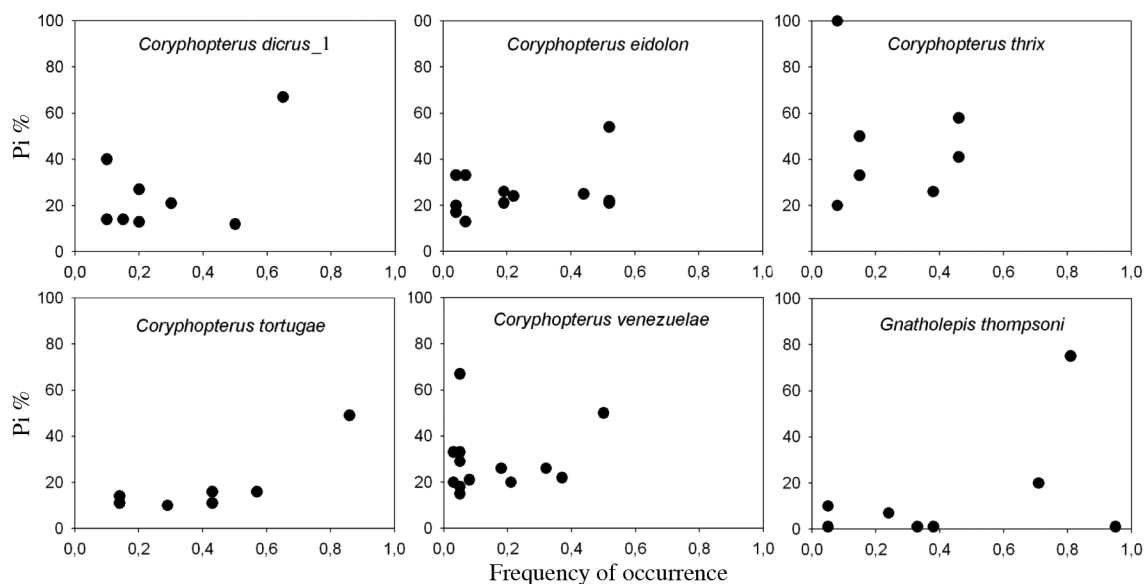


Figure 9. - Graphical analysis of data obtained from diet analysis. Pi is the prey specific abundance which is plotted against the frequency of occurrence.

Observations on feeding behaviour

All *Coryphopterus* species were observed to feed from the substrate as well as the water column; *G. thompsoni* feeds exclusively from the substrate. On days with strong currents or waves, all *Coryphopterus* species were observed feeding from the water column more often than on days with

little water movement; the same was found for days with decreased water visibility, i.e., many particles suspended in the water column. Results are summarized in table III indicating that differences between individual fish of the same species are considerable and size and sex also play a role in feeding behaviour. The χ^2 test (phi, Cramer's V) resulted in a

Table III. - Observations on the behaviour of *Coryphopterus* and *Gnatholepis*. Values represent means \pm standard deviation. See text for methods of assessment.

Species	TL [cm] (estimated)	Sex	Feeding from water	Feeding from bottom
<i>C. dicrus</i>	2.5	f	1 \pm 0	7 \pm 2
<i>C. dicrus</i>	3.0	m	5 \pm 1	3 \pm 1
<i>C. dicrus</i>	5.0	m	1 \pm 2	6 \pm 2
<i>C. cf glaucofraenum</i>	2.5	-	5 \pm 2	6 \pm 2
<i>C. cf glaucofraenum</i>	5.0	m	18 \pm 7	3 \pm 1
<i>C. thrix</i>	5.0	f	1 \pm 0	3 \pm 2
<i>C. thrix</i>	5.0	m	2 \pm 1	0 \pm 0
<i>C. eidolon</i>	2.0	-	13 \pm 5	2 \pm 0
<i>C. eidolon</i>	4.0	-	2 \pm 2	4 \pm 2
<i>C. eidolon</i>	5.0	m	1 \pm 0	2 \pm 1
<i>G. thompsoni</i>	3.0	-	0	134 \pm 42
<i>G. thompsoni</i>	4.5	-	0	72 \pm 17

significant relationship between time of the day and feeding ($p = 0.027$) only for one of all observed fishes (*C. thrix*, m, TL = 5 cm).

DISCUSSION

Teeth in the upper and in the lower jaw in all investigated *Coryphopterus* species are arranged very similarly, differing only in the number of rows and consequently in the number of teeth, but no morphological differences could be found. Differences in shape and size of teeth among the species, could probably be attributed to the size differences and does not show inter specific marks. In *C. tortugae* a difference between number of teeth of males and females were found; the female fishes, which were smaller in size, had a far smaller number of teeth in the lower jaw, but not in the upper jaw. Numbers of teeth counted in the lower and upper jaws as well as the pharyngeal tooth plates were similar within the five *Coryphopterus* species studied.

Böhlke and Robins (1960) described *C. dicrus* with six to seven rows of teeth (in the present study five to six rows), *C. thrix* with approximately six (five in the present study) and *C. eidolon* with five to six rows (four to five in the present study). For *C. tortugae* and *C. venezuelae* no data on dentition were available. The rows of teeth in *Coryphopterus* species are often poorly defined and therefore hard to count and could vary among different sampling locations. Similar results, including shape and arrangement of teeth, have been found among species of gobies in the Mediterranean Sea; intra-specific differences in numbers of teeth were observed from different sampling locations and could not be explained by size or sex of the fish (Pölzer and Patzner, 2000; Herler *et al.*, 2006).

Pharyngeal teeth among the *Coryphopterus* species were

very similar in shape and arrangement; they have not undergone any specialization in the different species. The pharyngeal tooth plates are a structurally complex apparatus, which are primarily used to separate food from unwanted material, manipulate prey and process it (Vandewalle *et al.*, 1994; Wainwright, 2006). The teeth can be independent of the oral jaws and thus have a potential autonomy in evolution, which widens the feeding abilities of fish. An important function of those teeth, which have undergone reorganization and specialization within various groups of perciform fish, is the ability to either crush hard shelled prey types like molluscs or punch holes into their shells allowing the digestive juices to reach the internal soft part after swallowing. Most studies on differentiation and function of pharyngeal teeth have been conducted in cichlids and labrids and linked to the specific feeding mode of each species (Vandewalle *et al.*, 1994; Clifton and Motta, 1998; Greven *et al.*, 2005; Wainwright, 2006).

In all the examined *Coryphopterus* species two separate bones compose the lower pharyngeal tooth plates. These bones are located very close together but lack a complete union. Parenti and Thomas (1998) reviewed the pharyngeal tooth plates of sycidiine gobies and several of their allies in the Pacific and found that in *Gnatholepis* the fifth ceratobranchials are united while in other species they remain separate. Larson (2001) made the same observation on *Gnatholepis* sp. in the Pacific; the present study confirms these results and leads to the conclusion that this probably presents a synapomorphy in the genus.

Coryphopterus spp. and *Gnatholepis thompsoni* differ in their feeding habits and prey; *Coryphopterus* species were observed preying on small benthic animals from the soil and water column, while *G. thompsoni* was almost continuously sieving through the sand. This could be confirmed by the observations made in the field and stomach contents analysis, which further on showed that prey groups were unequally represented in the stomachs of *Coryphopterus* species. Morphological studies can not be relied on to predict the diet of fishes; generally some characters of the oral jaws allow assumptions about prey items of fishes, but in many cases no reliable results can be obtained (Kotrschal, 1989; Clifton and Motta, 1998). Morphological structures in feeding of Chaetodontidae could be found to be correlated with how those fish feed rather than on what they feed (Motta *et al.*, 1995). Another study on the feeding apparatus of Labridae came to the conclusions that some of the morphological factors examined could be used for predicting diets, but most could not (Clifton and Motta, 1998).

Previous to this study no information was available on the prey items of *Coryphopterus dicrus*, *C. thrix* and *C. venezuelae*, whereas *C. eidolon* was reported to feed primarily on benthic algae and other plants (Pattengill *et al.*, 1997). Analyses of the digestive tracts of *C. tortugae* found detritus, sand, filamentous algae, foraminifers, nematodes and fish

eggs (Garzón-Ferreira and Acero, 1990). An analysis for *G. thompsoni* indicated similar results, with a large percentage of algae and detritus and a small proportion of copepods, amphipods, ostracods as well as unidentified crustaceans in the stomachs (Randall, 1967). An ecologically similar, congeneric species, *Coryphopterus* cf. *glaucofraenum*, which is often found in the same habitats, has been considered to be chiefly herbivorous and only to a lesser degree a carnivore, feeding on bivalves, ostracods, ophiuroids and copepods among the prey items (Randall, 1967; Wayman, 1973). Differences in prey items found in this and previous studies could be due to differences in collection sites (prey availability) and different data analysis (% volume). It appears that algae and plant material have been overestimated in their contribution to the diet, when compared to the results of the present study, and are not a primary food source, as previously assumed.

This is in accordance with the findings in this study where those species were found to prey on similar food and therefore might have similar dentition (Goldschmid *et al.*, 1980; Motta, 1985; Motta *et al.*, 1995; Galis and Drucker, 1996; Clifton and Motta, 1998; Parenti and Thomas, 1998; Westneat, 2006).

Though copepods were found to be important in number and occurrence, the importance of big prey items such as mysids or fish must be taken into account: they are represented in low numbers, but their nutritional value can be higher than a larger number of small organisms. The number of food items or their parts which are slowly digested remain more abundant and might bias the results of food analysis, depending on the methods applied for its description (Berg, 1979). The role of crustaceans in the diet might actually be lower than it seems in the present study because parts of their carapaces remain in the guts and are easily recognizable, while other items which digest quickly could have been recorded as unidentified material, after a similar time of digestion. Other food items can leave little or no recognizable remains and as a matter of different digestion speeds not accumulate in the same proportions in which they were ingested (Windell and Bowen, 1978). The two main findings concerning the diet of the investigated gobiids are: (1) they are carnivores and not primarily herbivores as reported previously; and (2) they can be considered generalized feeders with overlapping prey spectra differences between species and individual feeding strategies in *Coryphopterus* and whereas individuals of *G. thompsoni* use many resources at the same time. *Coryphopterus* species have similar food sources and therefore they are hardly competing for food; they probably occupy well defined microhabitats. *G. thompsoni* in contrary has different food sources which enables the species to live among *Coryphopterus* species on the sand patches of coral reefs.

Investigations will need to determine microhabitats for

the *Coryphopterus* species and the availability of prey items within those habitats to show how certain food categories are selected for. Geographical variation, feeding selectivity and ontogenetic shift in feeding strategies between populations of the same and different *Coryphopterus* species remain topics for future studies.

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